as *E. pilulifera* L. (Wheeler, 1941). Since *E. hirta* is a very widespread taxon and has become established as a weed in many regions, it is not unreasonable to suspect that it may have undergone localized aneuploidy. Before such an explanation is accepted, however, identity of plants from which previous reports were made needs to be checked. If the various reports do, indeed, all apply to the same taxon as currently recognized, the systematics and evolution within this group would make an interesting topic for future work.

The great variety of chromosome numbers in *Euphorbia* subg. *Chamaesyce* in North America is indicative of the very significant role that chromosomal changes have had in the evolution of these taxa. More reports from additional taxa and from additional populations will be needed before evolutionary relationships in subg. *Chamaesyce* can be satisfactorily elucidated.

Acknowledgments

I thank Ms. Meredith Lane and Mrs. Elinor Lehto for collecting plant material for this study. I am particularly grateful to Dr. Donald J. Pinkava for providing laboratory facilities for this investigation and for reviewing my manuscript.

Literature Cited

Beeks, R. M. 1955. Improvements in the squash technique for plant chromosomes. Aliso 3:131–134.

Hans, A. S. 1973. Chromosomal conspectus of the Euphorbiaceae. Taxon 22:591–636.

Johnston, M. C. and B. L. Turner. 1962. Chromosome numbers of *Dyssodia* (Compositae-Tagetinae) and phyletic implications. Rhodora 64:2–15.

Strother, J. L. 1969. Systematics of *Dyssodia* Cavanilles (Compositae: Tageteae). Univ. Calif. Publ. Bot. 48:1–88.

Urbatsch, L. E., J. D. Bacon, R. L. Hartman, M. C. Johnston, T. J. Watson, and G. L. Webster. 1975. Chromosome numbers for North American Euphorbiaceae. Amer. J. Bot. 62:494–500.

Wheeler, L. C. 1941. *Euphorbia* subgenus *Chamaesyce* in Canada and the United States exclusive of southern Florida. Rhodora 43:97–154, 168–205, 223–286.

GROWTH FORMS OF LARREA TRIDENTATA

Leonel Sternberg
Department of Biology, University of California, Riverside 92052

The population dynamics of *Larrea tridentata* have been of considerable concern to plant ecologists. Interest has centered around questions of geographical distribution (Shreve, 1942; Gardner, 1951; Yang, 1953; Rickard and Murdock, 1963; Beatley, 1974), spacing of individuals (Barbour, 1969a; Woodell et al., 1969; Wright, 1970), seed germination and seedling establishment (Knipe and Herbel, 1966; Barbour 1968; Sheps, 1973), and growth patterns (Spalding, 1904; Runyon,

1934; Wright, 1970; Vasek and Barbour, in press). Growth patterns of *Larrea* shrubs and response to environmental stresses have been described in developmental terms by Runyon (1934), Johnson et al. (1975), Wright (1970), and Vasek and Barbour (in press). In the Mojave Desert, circles of *Larrea* shrubs surrounding "bare" areas have been observed by Vasek et al. (1975), who interpreted these formations as clonal rings. Different developmental stages were noted from single-stemmed seedlings and large clumps to rings of satellite clumps. Clonal rings usually occur on mounds raised a few decimeters or so above general terrain level. Similar mounds were observed in Arizona by Wright (1970) who suggested several possible modes of origin.

Two questions about creosote rings immediately arise: (1) are they in fact clonal? and (2) what is their longevity? If they persist for extreme periods and undergo fragmentation, the definition of an individual *Larrea* shrub becomes problematical (Vasek and Barbour, in press). The purpose of this paper is to test whether rings are indeed clonal and to assess probable longevity. Members of a clonal ring by definition should be genetically identical whereas seedlings should be genetically diverse. Isoenzyme analysis provides a convenient test for genetic identity (Brewer and Sing, 1970).

Material and Methods

Study Sites

Observation and samples of rings were made at Lucerne Valley and Johnson Valley, San Bernardino County, California. Those two sites are located north of the San Bernardino Mountains and south of the Fry Mountains and Ord Mountains. The Lucerne Valley site has a sandy soil and may receive considerable drainage water from the San Bernardino Mountains. The Johnson Valley site has a rockier soil than Lucerne Valley and its elevated topography in a basin removed from the San Bernardino Mountains precludes drainage input. Thus, vegetation in the Johnson Valley site seems to be under more xeric conditions than that in the Lucerne Valley. The predominant plant community occurring in the two sites is a creosote bush scrub community with *Larrea tridentata* and *Ambrosia dumosa* (nomenclature follows Munz, 1974) occurring as dominants. A few additional observations and samples of some creosote rings were made in Death Valley (Inyo County, California) and Indio Hills (Riverside County, California).

Field Methods

Eight rings and 20 seedlings were sampled in Lucerne Valley and Johnson Valley. Leaf samples from a ring were collected from satellite shrubs at subjectively chosen points around the ring. Voucher specimens were not collected; however, the sampled creosote rings were marked and are available for further verification. Samples of seedlings were taken at the Lucerne Valley site in a 20 m^2 plot from young shrubs that had not yet

developed a root crown, thus the possibility of sampling two individuals from a clone was avoided. Leaf samples were placed in plastic bags immersed in ice and taken to the laboratory for isoenzyme assay. Isoenzyme assay was performed approximately 24 hours after collection of samples. The average radius of rings in Lucerne Valley and Johnson Valley was measured. Other putative clones were sampled for isoenzyme assays: one in Death Valley and two in Indio Hills.

Laboratory Analysis

Two enzyme systems from leaf extract were used in this study: peroxidase and acid phosphatase. Leaf material was washed with 95 percent ethanol and rinsed with water. Washed leaf material was ground with an equal weight (1.25 g) of sand and 3 ml of acetate buffer (pH 5.4; 0.1 M) into a homogeneous paste. This paste was centrifuged for 20 minutes at 10,000 r.p.m. The supernatant was saved and the pellet discarded. A 12 percent sucrose solution was made with the supernatant, and 15 μl of this solution were used for electrophoresis. Electrophoresis was done in 7.5 percent acrylamide gel (pH 8.9) for 3 hours with a tris glycine buffer (pH 8.3). The staining procedure for the peroxidase and acid phosphatase isoenzymes followed Brewer and Sing (1970) and Burstone (1962) respectively.

Results

The probable development of creosote rings can be observed in the field. A continuous series of stages occurs from single stemmed seedlings to large clumps with dead branches in the center to circles of satellite clumps. A continuous ring is probably an intermediate stage in this developmental sequence. An overhead view of a continuous ring shows a sterile center, the canopy, and the exterior of the ring (see photo in Vasek and Barbour, in press). A continuous ring occurs on a mound of sand at a slightly higher elevation than the surrounding soil surface. The mound has a loose sandy surface layer while the intermound soil has a more gravelly surface. Tunnels produced by animal activity are often found in the sandy mound both in the central area and in the periphery of the ring. In the outer edge of the sand mound, a mass of both living and dead root crowns is present. Root growth occurs predominantly outward, away from the center of the ring. Roots vary in length up to and sometimes longer than 3 m. Occasionally dead pieces of root crown are found in the sterile center of small rings. Using radio carbon techniques, growth rates for rings have been estimated under the assumptions that a ring is clonal and that dead root crown in the sterile center represents original material from the clone. Two rates were derived reflecting different ring growth rates under different environmental conditions. On a south-facing rocky slope, the growth rate was about 0.26 mm of radius per year (Vasek et al., 1975) and on a sandy substrate with relatively more mesic conditions, the growth rate was about 1.43 mm of radius per year (Vasek and Johnson, unpublished data).

Different types of creosote rings found in Johnson Valley and Lucerne Valley are shown in Figure 1. Fragmented rings may consist of only one large fragment giving them a "horseshoe" shape (fig. 1 B) or they might have many fragments (fig. 1 C). Secondary rings (sub-rings) growing from a primary ring are also shown in Figure 1. The primary ring can be either continuous (fig. 1 D) or fragmented (fig. 1 E). Other types of rings observed in the field are permutations of growth forms shown in Figure 1.

A total of 15 isoenzymes was found for the peroxidase system and six isoenzymes were noted in the acid phosphatase system. Representative zymograms of the peroxidase and acid phosphatase isoenzymes found in this study are shown in Figure 2. Figures 3 and 4 show zymograms of assays done for ten seedlings and for a creosote ring respectively. Each vertical row of bands represents an individual genotype with respect to the particular system used.

Discussion and Conclusions

Based on seedling samples, the probability of two individuals having the same genotype for peroxidase is 0.15 and that for acid phosphatase is 0.30. If the genetics of these two systems are independent of each other, then the probability of two seedling individuals having identical genotypes for both systems is 0.045. A survey of 20 seedling samples indicated that no individuals had identical isoenzymes for both peroxidase and acid phosphatase systems. This survey therefore provides evidence supporting the basic assumption that any two seed-derived individuals will probably differ in at least one isoenzyme system. *Larrea* is probably self-compatible (Hunziker et al., 1972), and thus could produce electrophoretically identical progeny by self-pollination. However, this is unlikely since genetic homogeneity was not seen in the seedling samples. In addition, a high degree of homozygosity would be required for a self-compatible plant to produce electrophoretically identical progenies. By negation of the proposed assumption, if two individuals contain identical isoenzymes for both systems they probably were not derived from different seeds; therefore they are clonal.

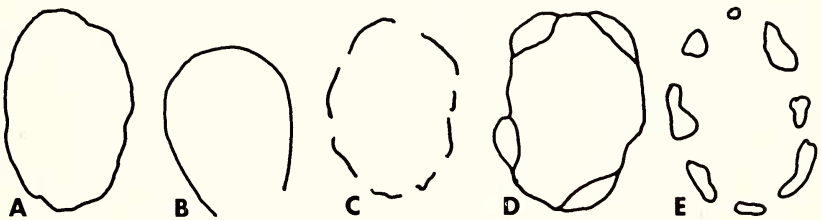

Fig. 1. Types of creosote rings found in Johnson Valley and Lucerne Valley. A=continuous creosote ring, B=creosote ring with one fragment only, C=ring with many fragments, D=secondary rings growing from a continuous primary ring, E=secondary rings growing from a fragmented primary ring.

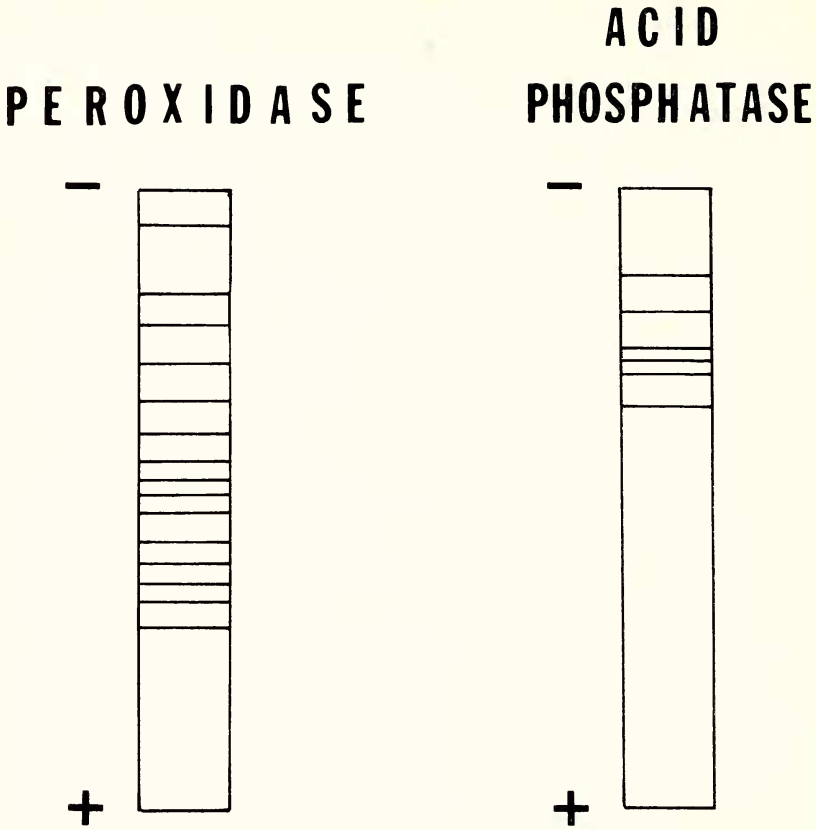

FIG. 2. Representative zymograms showing the locations of all isoenzymes found in the peroxidase and acid phosphatase systems.

The zymogram of assays done for a creosote ring (fig. 4) indicates that samples from the ring have identical isoenzymes for both systems; hence this particular ring is probably clonal. The analysis of other putative clones is given in Table 1. A few sample sets were assayed only for the peroxidase system. The probability of four or more individual seedlings having identical genotypes for the peroxidase system is very small. Thus, these sample sets are probably clonal (sample sets 2, 5, and 7) or partly clonal (sample set 10). The clonal process in Avra Valley, Arizona, has been described as either root sprouting, stem layering, or crown splitting (Wright, 1970). In the sites studied here, only crown enlargement and fragmentation were observed as clonal processes.

The choice of hypothetical clones (Table 1) was based on aerial photographs and ground level inspections. Aerial photographs were not always sufficient to determine whether growth forms were clonal. From an aerial photograph the clumps in sample set 1 (Table 1) appeared to be

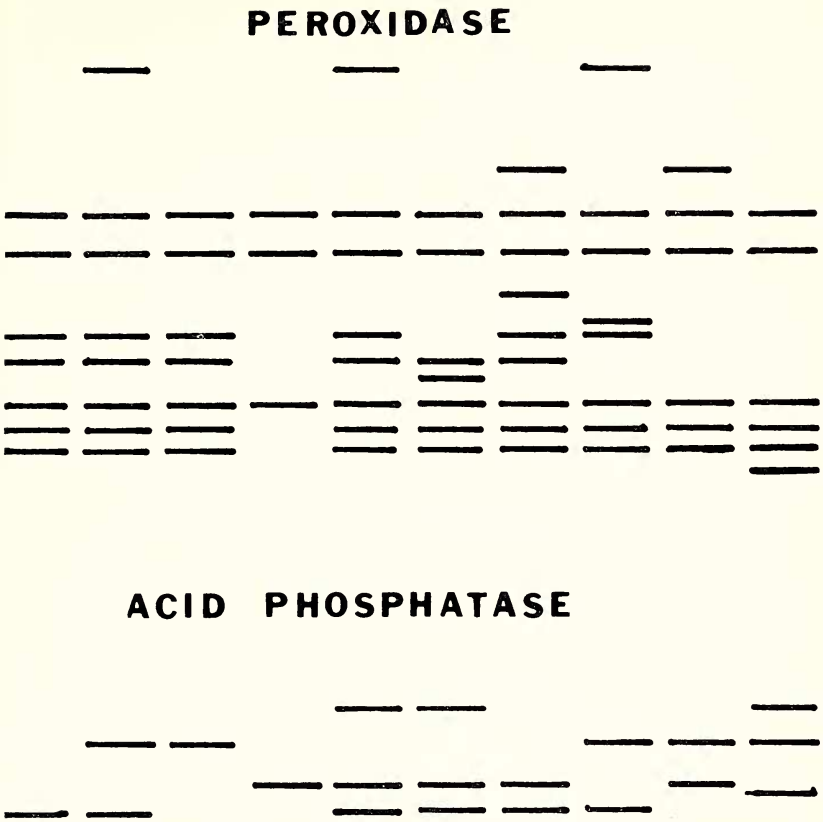

FIG. 3. Zymogram of 10 seedling samples for the peroxidase and acid phosphatase system.

in a circular pattern, but ground level inspection of clump arrangement indicated the pattern was not circular and thus these clumps probably did not have a common clonal origin. Isoenzyme analysis showed that these clumps had different genotypes, which confirms ground level interpretation of growth forms. A variety of clonal growth forms was tested as shown in Table 1. All continuous rings were clonal; however, fragmented rings were either clonal or showed a mixture of clonal and seedling material. Mixture of seedling and clonal material probably represents the germination of seeds and establishment of seedlings in the vicinity of an established shrub. Wright (1970) suggests that the microenvironmental conditions in the vicinity of an established shrub might favor the germination of seeds in its vicinity.

All sites studied here had a more or less sandy substrate; hence the growth rate of 1.43 mm of radius per year is more representative of the growth rates of rings measured in Lucerne Valley and Johnson Valley. The results are shown in Table 1. In Johnson Valley, age approximations

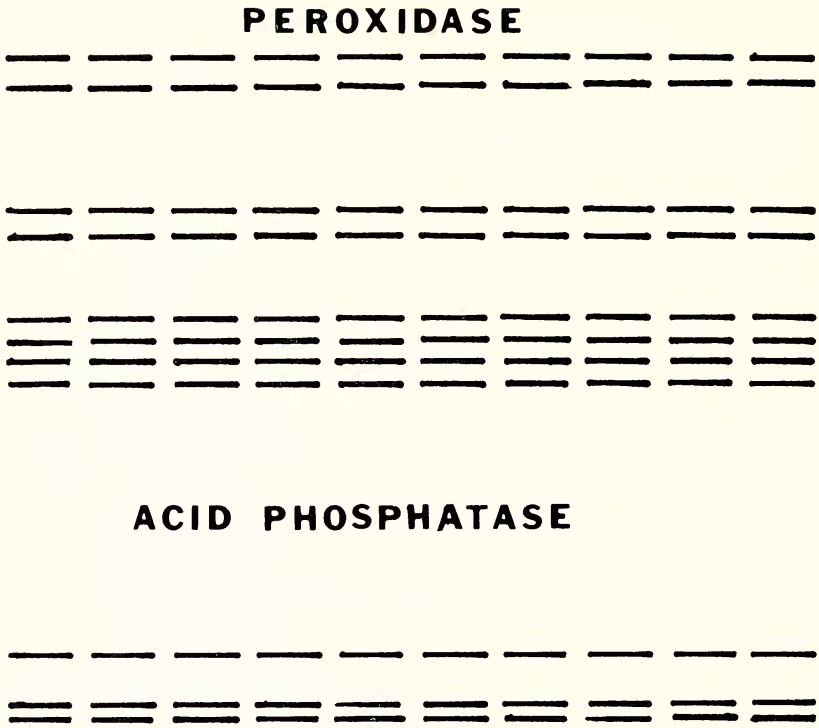

FIG. 4. Zymogram of 10 samples from a creosote ring for peroxidase and phosphatase system.

are probably a minimum estimate of age, since the environment is relatively more xeric than that in Lucerne Valley.

Several stages in the development of a creosote ring are documented in Table 1. Sample set 2 was a large clonal clump. Senescence in the center of a clump produces a clonal ring (sample set 3). Fragmentation of a clonal ring is the probable cause in the formation of a ring of satellite clumps (sample sets 7 and 8). Establishment of new genetic material in a creosote ring might occur at a later stage in the life history of a creosote ring (sample sets 9, 10, and 11). At any stage in this developmental sequence, there is variation in the average radius of rings and consequently in the approximate age of rings. Thus, sample set 8 is older than sample set 3 in developmental terms but younger in approximate chronological age. The observed disparity between developmental and chronological ages indicates that the shaping of these developmental forms is dependent on factors other than the radial growth.

The clonal abilities of *Larrea* may be relevant to several aspects of population dynamics. Sheps (1973) indicated in a study of seed germination in *Larrea* that survival of *Larrea* in nature might involve factors

Table 1. Characteristics of Growth Forms of Creosote Bush. Growth forms A through E are shown in Figure 1. *Sample could not be visualized as being a ring of satellite clumps from ground level. **Leaf sample was assayed for peroxidase system only. ***Radius not measured. †Age estimated with growth rate of 1.43 mm of radius per year.

Sample set	Type of growth form	Number of samples	Number of fragments	Average radius in m	Number of genotypes	Location	Estimated age in years†
1	*	10	10	—	10	Johnson V.	—
2	Clump	4	—	—	1**	Death V.	—
3	A	10	—	4.4	1	Johnson V.	3077
4	D	12	—	7.8	1	Johnson V.	5454
5	D	6	—	1.7	1**	Johnson V.	1189
6	B	8	1	2	1	Lucerne V.	1399
7	C	4	2	—	1**	Indio	***
8	C	4	3	1.5	1	Johnson V.	1049
9	B	2	1	2.5	2	Lucerne V.	—
10	C	8	2	—	2**	Indio	—
11	E	8	5	3.6	2	Lucerne V.	—

other than seed germination. The clonal abilities of *Larrea* might be one important factor contributing to the survival of *Larrea* in nature. Cloning in *Larrea* allows the perpetuation of a population to be independent of the hazardous process of seed germination (Muller, 1951). Age estimations of clonal rings indicated that the vegetative persistence of *Larrea* is enormous. The longevity of *Larrea* clones, as in all long-lived clones, might preserve a population in which an advantageous mutation has arisen (Muller, 1951). The survival of three chromosomal populations in *Larrea* (Barbour, 1969b) could have been favored by this longevity. Another aspect related to the clonal abilities of *Larrea* is the distribution of individuals in a population. Since cloning obscures any precise identification of an individual, an arbitrary definition of an individual by different authors could have contributed to contradictory results in pattern studies of *Larrea* (King and Woodell, 1973; Barbour, 1973; Anderson, 1971).

Acknowledgments

I am grateful to Dr. F. C. Vasek for introducing me to this problem and for his helpful suggestions in preparation of this manuscript. I am equally grateful to Dr. H. B. Johnson for his help and guidance during the investigation.

Literature Cited

Anderson, D. J. 1971. Pattern in desert perennials. J. Ecol. 59:555–560.

Barbour, M. G. 1968. Germination requirements of the desert shrub *Larrea divaricata*. Ecology 49:915–923.

———. 1969a. Age and space distribution of the desert shrub *Larrea divaricata*. Ecology 50:679–685.

———. 1969b. Patterns of genetic similarity between *Larrea divaricata* of North and South America. Amer. Midl. Naturalist 81:56–67.

———. 1973. Desert dogma reexamined: Root/shoot productivity and plant spacing. Amer. Midl. Naturalist 89:41–57.

Beatley, J. C. 1974. Effects of rainfall and temperature on the distribution and behaviour of *Larrea tridentata* in the Mojave desert of Nevada. Ecology 55: 245–261.

Brewer, J. C. and F. C. Sing. 1970. An introduction to isoenzyme techniques, Academic Press, New York.

Burstone, M. 1962. Enzyme histochemistry and its application to the study of neoplasm. Academic Press, New York.

Gardner, J. L. 1951. Vegetation of the creosote bush area of the Rio Grande Valley in New Mexico. Ecol. Monogr. 21:379–403.

Hunziker, J. H., R. A. Palacios, A. G. de Valesi, and L. Poggio. 1972. Species disjunctions in *Larrea*: evidence from morphology, cytogenetics, phenolic compounds, and seed albumins. Ann. Missouri Bot. Garden 59:244–233.

Johnson, H. B., F. C. Vasek, and T. Yonkers. 1975. Productivity diversity and stability relationship in Mojave desert roadside vegetation. Bull. Torrey Bot. Club 102:106–115.

King, T. J. and S. R. J. Woodell. 1973. The causes of regular patterns in desert perennials. J. Ecol. 61:761–765.

Knipe, D. and C. H. Herbel. 1966. Germination and growth of some semidesert grassland species treated with aqueous extract from creosote bush. Ecology 47:775–781.

Muller, C. H. 1951. The significance of vegetative reproduction in *Quercus*. Madroño 11:129–137.
Munz, P. A. 1974. A California flora and supplement. Univ. California Press, Berkeley.
Rickard, M. H. and J. R. Murdock. 1963. Soil moisture and temperature survey of a desert vegetation mosaic. Ecology 44:821–824.
Runyon, E. H. 1934. The organization of the creosote bush with respect to drought. Ecology. 15:128–138.
Sheps, L. O. 1973. Survival of *Larrea tridentata* S&M seedlings in Death Valley National Monument, California. Israel Bot. 22:8–15.
Shreve, F. 1942. The desert vegetation of North America. Bot. Rev. 8:195–246.
Spalding, V. M. 1904. The creosote bush (*Covillea tridentata*) in its relation to water supply. Bot. Gaz. (Crawfordsville) 38:122–138.
Vasek, F. C. and M. G. Barbour. in press. Mojave desert scrub vegetation. Chapter 24 in Terrestrial vegetation of California (J. Major and M. G. Barbour, eds). Wiley Interscience, New York.
————., H. B. Johnson, and D. H. Eslinger. 1975. Effects of pipeline construction on creosote scrub vegetation of the Mojave Desert. Madroño 23:1–13.
Woodell, S. R. J., H. A. Mooney, and A. J. Hill. 1969. The behavior of *Larrea divaricata* (creosote bush) in response to rainfall in California. J. Ecol. 57: 37–44.
Wright, R. A. 1970. The distribution of *Larrea tridentata* (D. C.) Coville in the Avra, Arizona. J. Arizona Acad. Sci. 6:58–63.
Yang, T. W. 1953. Distribution of *Larrea tridentata* in Tucson area as determined by certain physical and chemical factors of the habitat. J. Range Manage. 6:158.

REGENERATION OF INTRODUCED SPECIES OF CISTUS (CISTACEAE) AFTER FIRE IN SOUTHERN CALIFORNIA

Kenneth R. Montgomery
Research Division, Los Angeles State and County Arboretum
Arcadia, California 91006
Thomas W. Strid
Department of Botany, University of Georgia, Athens 30602

Establishment of vegetative cover for erosion control on barren or disturbed wildland sites is an important aspect of watershed management in Southern California. Disturbances resulting from construction activities pose a particularly serious problem. Early attempts to extend the cover provided by native chaparral shrubs onto these sites by direct seeding and transplants were of only limited success (Juhren, 1956). A number of introduced shrubs from areas of similar Mediterranean climate were subsequently tested to find species that might perform more satisfactorily in low-maintenance plantings (Juhren, 1956; Hellmers and Ashby, 1958; Ching, 1959).

Among the most promising introductions were species of *Cistus* (rockrose) native to the Mediterranean Basin (Juhren, 1956). These